

On 'Bridging the Gap between Race and Species': The Isolation Concept and an Alternative

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(Communicated by T. G. VALLANCE)

LAMBERT, D. M., & PATERSON, H. E. H. On 'Bridging the gap between race and species': The isolation concept and an alternative. *Proc. Linn. Soc. N.S.W.* 107 (4), (1983) 1984: 501-514.

This contribution examines some aspects of the current state of studies on species and speciation. In particular, the role which Dobzhansky's Isolation Concept has played in the development of theories is briefly reviewed and the validity of some current commonly-accepted views are examined. A new species concept, the Recognition Concept, is discussed in the light of serious objections to these current views. We examine some aspects of the reinforcement model, especially the relationship between this model of speciation and the Isolation Concept of species. Some predictions of the Recognition Concept are detailed, and contrasted wherever possible, with alternative predictions of the Isolation Concept. Finally, it is suggested that the testing of these alternative predictions is of paramount importance.

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INTRODUCTION

It is twenty-three years since the publication of Theodosius Dobzhansky's paper 'Bridging the gap between race and species', in the Proceedings of the Linnean Society of New South Wales (1960). This was the second Sir William Macleay Memorial Lecture, and Dobzhansky, firmly recognized as one of the leading evolutionary biologists of the time, presented a knowledgeable and authoritative account of current evolutionary research. In this paper Dobzhansky recounted his understanding of the relationship between races and species and made important comments on the nature of species and of speciation. After twenty-three years, and eight years since the death of this most influential biologist it seems an appropriate time to reflect on the current theoretical corpus, and consider what changes may have occurred in our thinking since that time.

THE CURRENT PARADIGM

Theodosius Dobzhansky, by his succession of classic books (1937, 1951, 1970) and his innumerable articles, greatly influenced the genetic study of evolutionary biology for approximately four decades (Ruse, 1981: 810). Ernst Mayr (1970) described him as the '... foremost architect of evolutionary genetics of today'. Dobzhansky left behind him, besides the residues of his own personal influence, a large number of students of particular ability. Many of these students have helped to further develop Dobzhansky's original ideas, and the well-known textbook 'Evolution' (1979), written with a number of co-workers, summarizes much of the general thinking of the 'Dobzhansky School'.

Amongst his most significant innovations Dobzhansky will be remembered for his introduction of the term 'Isolating Mechanisms' (Dobzhansky, 1937). It is perhaps not immediately apparent the degree to which this term has influenced the development of our ideas. However, on reflection, this is the basis of the Isolation Concept of species,

as Paterson (1980) has named it, and the listing of 'pre mating and post mating Isolating Mechanisms' (Mecham, 1961) gave biologists one of the most useful conceptual frameworks on which to hang ideas and use as a basis for data collection.

Dobzhansky viewed a species as any group of individuals which is 'reproductively isolated' from any other group. This inevitably influenced his concept of speciation which is, logically, the development of these 'Isolating Mechanisms'. Although Dobzhansky (1960) commented that '... the means whereby speciation is accomplished, i.e. whereby reproductive isolating mechanisms are established between diverging populations, are not the same in all organisms', he nevertheless argued consistently over many years, for one particular model of speciation. This model has been referred to as 'Speciation by Reinforcement' (Grant, 1966).

Reinforcement requires the evolution of 'pre mating isolating mechanisms' through the direct action of natural selection. This is supposed to occur when populations secondarily overlap and hybrids between individuals of the two groups are disadvantageous. Selection then favours individuals that mate only with their own group, since those which crossmate are reproductively penalized owing to the reduction in fitness of hybrids. This is what Dobzhansky meant when he said '... the hybrid sterility caused by the peculiar cytoplasmic effects was probably the primary, and the sexual isolation the secondary, reproductive isolating mechanism in *D. paulistorum*' (1960). Ayala (1975) agreed with this view, and in his discussion of the subject commented: 'The process of speciation is being completed between the semi-species. Sexual Isolation is being superimposed over the pre-existing hybrid sterility and is nearly complete in many cases . . .'

It cannot be emphasized too strongly that there is a distinct logical nexus between the term 'Isolating Mechanism' and the Reinforcement model of speciation. If natural selection directly causes the evolution of divergent courtship patterns for the function of isolation, then these should indeed be considered 'Mechanisms' (*sensu* Williams, 1966) to isolate. If one does not necessarily accept that particular model of speciation, then the term is inconsistent and hence inappropriate. For example, if one agrees that there is overwhelming evidence that species arise as a result of allopatric divergence, and that secondary overlap of population is not a prerequisite for speciation, then characteristics such as courtship behaviour and the structure of male and female genitalia should not be considered logically as 'Isolating Mechanisms'.

Dobzhansky's speciation model is discussed in some detail in his Macleay Lecture and he uses the results of his own work on *Drosophila paulistorum*, together with those of his colleague Lee Ehrman, to illustrate the concept. Since that time a number of other workers, and in particular Ehrman, have gone on to detail this interesting case and to establish it as a classical case in speciation studies (Ehrman, 1960, 1965; Dobzhansky *et al.*, 1969; Malogowokin *et al.*, 1965; Ayala, 1975). *Drosophila paulistorum* was described by Dobzhansky as a 'ring' species. He explains this as '... a series of races, the adjacent members of which resemble each other closely, and are often connected by intermediates in the geographically intermediate zones. But the terminal members of the "ring" live together, sympatrically, differ usually more strongly than do neighbouring races elsewhere in the "ring", and yet do not interbreed and do not form intermediates'. Dobzhansky (1960) referred to these six races as being '... mostly allopatric, occurring in different countries'. Today, however, these six 'semispecies' are known to overlap considerably (see fig. 2, Ayala, 1975). The example is no longer considered a case of a 'ring' species. However, it is accepted by many authors as a classic example of Dobzhansky's much advocated speciation model.

Although Dobzhansky's paper is twenty-three years old, his basic comments on *D. paulistorum* are still accepted by a great many biologists (e.g. Bush, 1975; Grant, 1963;

White, 1978). He set the scene for much future research and gave a broad framework within which many biologists would work for at least two decades.

We contend that essentially very little has changed in this aspect of evolutionary theory since that time. The advent of techniques for the analysis of enzyme variability for example may be considered by some to have been a significant change in direction. In retrospect, however, many discussions such as that of Ayala (1975), and Avise (1974), considering genetic differentiation during the speciation process, show that these data are merely plugged into the framework which Dobzhansky left behind.

The central concept considered by Dobzhansky in the paper under discussion, that of the relationship between species and races, is an old one. As he points out, Darwin considered species to be merely highly-developed varieties. This is perhaps one of the most basic ideas in speciation theory; that populations adapt to different environments and that speciation is a gradual process which is an indirect consequence of the process of differential adaptation. This is essentially the 'Dumbell Model' of speciation (White, 1978). A large population becomes divided, perhaps by some extrinsic barrier, and the two separated populations slowly diverge. Hence these populations go through the stages of varieties, to sub-species and finally distinct species. It was the presence of varieties and races which so impressed Darwin and which seemed to him to form a logical connecting link between populations of the one species and completely distinct species. Dobzhansky completed his paper by commenting, with respect to the *D. paulistorum* species, 'In any case, we have a beautiful demonstration of Darwin's argument that . . . species are only strongly marked and permanent varieties, and that each species first existed as a variety'. Herein lies a logical inconsistency in Dobzhansky's argument. Whilst he argues for the evolution of *D. paulistorum* species via reinforcement he immediately suggests that Darwin's gradualist speciation arguments are compatible with this view. These two speciation models are logically distinct and incompatible. Dobzhansky and his co-workers have however consistently argued that these views are indeed compatible. Dobzhansky (1970), for example, remarks 'The two hypotheses (reinforcement and allopatric change) are not mutually exclusive. Needless disputes have arisen because they were mistakenly treated as alternatives'. Some years later Dobzhansky *et al.* (1977) made essentially the same statement.

We disagree: Either natural selection *is* or *is not* capable of causing the evolution of complete divergence in 'pre-mating isolating mechanisms' of individuals of different populations.

After having argued very strongly against the reinforcement model in his earlier book (Mayr, 1942), Mayr (1963) changed his view and argued for a limited role for reinforcement. Thus he said, when considering hybrids 'Such hybrids, being sterile cannot reproduce and thus there is no danger of a breakdown of the species barrier. However, there will be strong selection in favour of the acquisition of additional isolating mechanisms to prevent such wastage of gametes' (p.551). This view is one held by many biologists — that of a limited role of natural selection in the perfection of isolating mechanisms. Mayr (1963: 551) says 'Nevertheless natural selection does play a role in the improvement of some of the isolating mechanisms, only it concerns subsidiary isolating mechanisms. The primary, basic one must be fully efficient when contact is first established'. However here lies the crux of this seemingly 'reasonable' view to hold. If the primary basic isolating mechanism is 'fully efficient' then where is the selective pressure to cause a change? Certainly if pre-mating mechanisms are 'fully efficient' then there are no cross-matings and hence no immediate pressure to direct the development of further isolating mechanisms. Mayr argues that this is so since he discusses species in which reproductive isolation is maintained exclusively by the

differences in display song. Since hybrids in the case he discusses (that of *Chortippus brunneus* and *C. biguttulus* (Perdeck (1957) quoted in Mayr, 1963) are quite fertile 'The function of this ethological isolating mechanism must have been virtually perfect before contact was established, because the essentially fully viable hybrids would serve as a channel of gene flow between the two species, if they occurred at all frequently'.

Hence we see that Mayr is indeed advocating essentially the same process as Dobzhansky. The argument is simply that this is a refining process which 'sharpen up isolating mechanisms'. We point out that when there is very little hybridization there is consequently very little selective pressure to cause divergence. If there is no divergence in the mate recognition systems of two populations then hybrids will form 50% of the F₁ generation and presumably a large percentage of subsequent populations. However if hybrids form only 1% of the population there is very little selective pressure to cause a change in the mate recognition systems. This remains an important problem, and one which is not addressed by advocates of reinforcement (Lambert *et al.*, 1984).

We would suggest that it is an appropriate time to re-analyse the direction that evolutionary theory has taken, consider the influence of Dobzhansky's school of thought and consider some recent developments.

THE RECOGNITION CONCEPT OF SPECIES

For a number of years Paterson (Paterson and Jantes, 1973; Paterson, 1976, 1978, 1980, 1981, 1982) has argued that the term 'Isolating Mechanism' is inappropriate and misleading. He has suggested an alternative species concept, the *Recognition Concept* and contrasted it to the Isolation Concept. The Recognition Concept emphasizes that species are groups of organisms which are tied together by a common *Specific-Mate Recognition System* (SMRS).

The SMRS is a communication system which results in conspecific fertilization: a subset of a broader category, Fertilization Mechanisms. Paterson's argument is that the phenomena known as 'Isolating Mechanisms' were not moulded by natural selection for the *function* (*sensu* Williams, 1966) of isolating one species from another, but should more appropriately be viewed as communication phenomena that result in fertilization. According to this view species are not the direct products of natural selection to isolate, they are incidental consequences of change in the SMRS of individuals of a population. Students of the Recognition Concept agree that species are 'isolated' from other species; however, this is purely an incidental effect of differences in the SMRS's and therefore, of little direct evolutionary importance.

The SMRS is a species-specific communication system comprising a unique signal-response chain. Different signals in the chain may be auditory, tactile, visual or olfactory for example. A close examination of biparental species demonstrates that individuals, from unicellular algae to mammals, ensure fertilization by the operation of a SMRS of this basic nature. Such a communication system can be described as being maintained by stabilizing selection since any individual which is a deviant with respect to its signal or receiver is less likely to be recognized by, or recognize, a conspecific mate (Lambert *et al.*, 1982; Lambert and Paterson, 1982). This has previously been pointed out (Paterson, 1976, 1978) and subsequently recognized by others (Carson, 1978; Templeton, 1979). Striking evidence for the stability in the mate recognition system of *Drosophila melanogaster* has recently been presented (Henderson and Lambert, 1982). Individuals from worldwide populations of this species appear to possess mate recognition systems which are not detectably different. This lack of variation in the SMRS is in marked contrast to the variation in other genetical and morphometric characteristics of these populations (details in Henderson and Lambert, 1982). Perhaps this is a feature of many species. Geographic variation in characters such as bird and

frog calls may *not*, in fact, be evidence for variation in mate recognition characteristics. Individuals almost certainly do not recognize the *call* as a mate recognition character but some *component* of that call. More intense study may show that certain parameters are quite geographically stable. The stability of the SMRS in large natural populations is amply demonstrated by experiments using sterile male insects released in order to eliminate target populations. One reason for the failure of control programmes of this type is changes in the mating behaviour of released males (Bush, 1978). Such altered males are not accepted for mating by females of the target population.

A VIABLE ALTERNATIVE?

The Isolation Concept has been a useful one for a long period of time in that it stimulated much biological research. However, if the phenomena described as 'Isolating Mechanisms' are not the products of natural selection moulded to keep species apart, but intraspecific communication phenomena, a reinterpretation of much previous thinking is needed. New questions must be asked. For example, how do communication systems operating between male and female individuals change? Is this not the essential problem of speciation? What are the laws which govern the transformation of one SMRS to a new and stable SMRS? Why is it that at speciation other species specific communication systems often appear to change also?

Immelmann's (1967) studies on Australian finch species yield an interesting example in this regard. In all these species chicks have patterning inside the mouth which are recognized by the adult bird and this system enables accurate placing of food in the mouths of young (see Immelmann, 1967: 8-9). Immelmann comments that these patterns are '. . . very distinct for a species, and for a group of closely related species, they are important features in the study of the bird systematics'. Adults of each species are 'attuned' to the conspecific patterning and this elicits the feeding response. It seems likely that the patterns are so constant because any chick deviant in its marking pattern will produce a weaker feeding response by the female and hence have less chance of surviving. Adults producing such a deviant chick will also suffer a reduction in their reproductive success.

In speciation events in this group of finches, not only has the SMRS changed, but this offspring-adult communication system also commonly changes. Perhaps studies dealing with other communication systems may yield important information regarding this general phenomenon.

If the SMRS remains stable as evidence indicates, then it is unlikely to change gradually over long periods of evolutionary time. Even if two large populations were gradually to change as a result of different environmental conditions, will the SMRS necessarily change? The condition most conducive to change in the SMRS appears to be small population size. Is then the process of speciation really reflected in the presence of varieties and subspecies? It may well be that large geographically separated populations which are commonly recognized as subspecies are not in the process of gradually changing their SMRS's and hence are not speciating. Whatever distinctness they may show could have occurred while the population was small, prior to its expansion.

The question might reasonably be asked: If the SMRS is so stable, how can it change at speciation? Under conditions of small population size changes in the SMRS can and do occur (Powell, 1978; Arita and Kaneshiro, 1979). Selection may, however, act to maintain the SMRS, and one sex may be selected to recognize the signals from individuals of the altered sex. This could then result in efficiency of communication. Such a process will cause changes in the SMRS of some small isolated populations such

that recognition between individuals of the parental and daughter populations does not occur. A speciation event has then occurred.

The Recognition Concept resolves problems that have been noticed by other authors. Levin (1979) for example is dissatisfied with the ability of the Isolation Concept to explain the nature of plant species. He has commented 'It is important to recognise that isolating mechanisms do not exist as properties of single species or single populations'. It is true that isolation is a characteristic only of at least two species never of one. Indeed, species in terms of the isolation concept is a 'relational concept' (Mayr, 1963). Mate recognition, however, is an individual phenomenon and therefore has meaning regardless of the presence of closely related species. Littlejohn (1981) has also recently argued against the concept of reproductive Isolating Mechanisms. Inherent in the Recognition Concept is that species are not in themselves deliberate adaptive devices of the biological world as some have believed (Dobzhansky, 1976; MacArthur and Connell, 1966; White, 1978) but incidental effects of the evolution of sexual reproduction. An examination of the Recognition Concept reveals its basic emphasis on the intraspecific nature of the male-female communication phenomenon. Any characteristic of species which is incidental to this important intraspecific phenomenon is also incidental to the essence of species. Since 'postmating isolating mechanisms' such as hybrid sterility cannot have been directly selected for (Darwin, 1859; Meham, 1961; Paterson, 1976), despite invoking selection to this end by some authors (e.g. Grant, 1966). Therefore they are not 'mechanisms' (*sensu* Williams, 1966) and their nature is an effect of allopatric change. Here again is a basic difference between the Isolation and Recognition concepts.

Dobzhansky (1960) believed that species arise via secondary overlap of populations which have acquired, in isolation, 'postmating isolating mechanisms'. He maintained that natural selection will directly cause the evolution of species. This will be achieved because individuals from the one group which mismate with individuals of another will have offspring which are disadvantageous (hybrid inviability). Over successive generations selection will favour individuals which recognize mates belonging to their own group and mate only with them. These 'mechanisms' which ensure that individuals do not mismate with members of another group will eventually be perfected by selection and at this time perfect 'isolation' will be achieved and the speciation event completed.

Dobzhansky's reinforcement model has recently been under critical examination from a number of authors. Paterson (1978) has argued that another important factor, that of heterozygote disadvantage, has not been considered and that this can conceivably lead to an alternative outcome. Moore (1957) and Mayr (1942) have criticized this model for a number of theoretical reasons and Futuyma and Mayer (1980), Jackson (1973), Loftus-Hills (1975), Paterson (1978), Roberts (1976), and Walker (1964), have recognized a scarcity of convincing cases in the literature. Moore's (1957) serious general criticisms have never been satisfactorily answered. Littlejohn (1981) appears to accept Moore's argument that genes which have been selected for divergent SMRS's in the zone of secondary overlap will be disadvantageous in allopatry. Indeed, as recognized by Wallace (1968: 377-378) the criticism raised by Moore is satisfied in the model of speciation by small population size developed by Carson (1955, 1975). Littlejohn's (1981) suggestion that reinforcement might still be possible when one population is completely surrounded by another and hybrids are disadvantageous, needs to be examined while taking into account the force of heterozygous disadvantage. The much more likely outcome of such a situation would be elimination of the rarer population (when $S = 1$ for hybrids) or a cause of the disadvantage (when 0

$< S < 1$) (Paterson, 1978, 1981). Harper and Lambert (1983) have recently presented experimental verification of the power of negative heterosis.

Despite the fact that Littlejohn (1981) did not consider the effects of negative heterosis on the vital process of selection for divergence, he apparently nevertheless considers the process can feasibly result in the evolution of distinct species (see his p.328). Littlejohn regards the following studies as detailed and requiring discussion: Blair, 1955; Littlejohn, 1965; Fouquette, 1975 and Ralin, 1977. We will now discuss these.

Fouquette, 1975:

Fouquette (1975) described an analysis of mating calls of two species of the frog genus *Pseudacris* and reports 'divergence' in two components of calls: pulse rate and pulse number. Fouquette (1975:19) argues that '. . . only the differences in mating call can be identified as an effective mechanism operant in maintaining integrity of these species'. The author then goes on to argue that in order to be able to demonstrate character displacement in sympatry it must be possible to determine which characters are used in call discrimination and then to show that differences in these are significantly greater in sympatry than in allopatry. The proposed method by which call parameters are designated as important illustrates a basic circularity in argument. Referring to pulse rate (Pr) of calls Fouquette (1975) comments 'If separate localities are examined (fig. 2e), the slowest *feriarum* call is faster than the fastest *nigrita* at all sympatric localities, by a factor of 2 or greater. *This suggests* that Pr is the critical component of mating call enabling females of this species — complex to recognise males of their own species' (our emphasis). The circularity here is that Pr is suggested to act as an isolating mechanism because, in sympatry, there is divergence in this character. However Fouquette's basic argument is that these data are evidence for the reinforcement of isolating mechanisms because the character shows divergence in sympatry. Clearly it must be possible to 'illustrate' reinforcement while using this logic. Whenever one finds a character which shows some evidence for divergence in sympatry it is therefore designated as an isolating mechanism and hence this is consequently evidence for divergence of an isolating mechanism in sympatry. Since divergence is the criterion on which it is designated as an isolating mechanism, to subsequently argue that this is now evidence for reinforcement is unreasonable.

In posing the general problem '. . . can character displacement be demonstrated in call components that are critical in enabling females to identify the call of their own species?' (Note that he has framed this in the positive or recognition format), he goes on to say 'To answer this we must determine what parameters are used in call *discrimination*, and ascertain if differences in these are significantly greater in sympatry than in allopatry' (our emphasis). The latter comment illustrates that Fouquette considers that certain call parameters will indeed be used not to recognize conspecifics as mates but to act as isolating mechanisms and allow the individual to discriminate against non-group members (an isolationist view). Fouquette admits however that 'No direct data are available for Chorus Frogs to indicate which part of the call may be utilized in discrimination . . .'

We agree with Fouquette that characters of calls which exhibit high variability are unlikely to be those involved in mate recognition. It is agreed that we must look for characters of rather low variability. However it is quite possible that one species e.g. *nigrita* uses pulse rate as a component of the mate recognition system and that *feriarum* uses some other component. Pulse rate cannot then be an isolating mechanism since, according to this scheme, individuals of *feriarum* do not use it to 'discriminate' against *nigrita* individuals. In general it is an isolationist assumption that two species will use the *same* call character to ensure there will be no cross matings. On the contrary it

seems likely that, of two closely related species, one might use one call parameter in mate recognition and the other might use a different parameter.

In conclusion because of Fouquette's circular reasoning and his lack of any evidence regarding which call parameters are used in mate recognition we argue that this cannot be regarded as evidence for reinforcement.

Ralin, 1977:

The study of Ralin (1977) discusses evidence for reproductive character displacement between populations of the North American frogs *Hyla chrysoscelis* and *H. versicolor*. Ralin (1977) argues that there are three results which are *sufficient* to infer that reproductive character displacement is occurring. These are (1) that call parameters '... differ significantly from sympatry to allopatry'; that (2) those same parameters '... differ in directions that increase the sympatric differences between two species' and (3) that they '... differ in a pattern that cannot be explained as the result of alternative factors'.

First we would however point out that evidence must be presented that these characters are involved in mate recognition. With respect to the particular case concerned, Ralin suggests that there is evidence for the reinforcement of pulse rate and call duration between these frog species. With respect to pulse rate he admits that females of the *H. chrysoscelis* — *H. versicolor* complex '... are capable of species specific discrimination at the level of the difference in mean pulse rates of any two populations of *H. chrysoscelis* and *H. versicolor* whether *sympatric* or *allopatric*' (our emphasis). If this is so there cannot be any pressure to cause sympatric divergence because there can be no mismating. Ralin hence goes on to produce an argument, unconvincing to us, that *chrysoscelis* females might still mate with *versicolor* males and hence reinforcing selection is argued to be possible. Although Ralin suggests that differences in call duration are being reinforced in sympatry he also acknowledges that there is a great deal of overlap in this call parameter between the two taxa.

Unlike Littlejohn (1978), Ralin (1977) does not consider the work of Blair (1955) as a convincing case of reinforcement. He considers only Littlejohn's work on the *Litoria ewingi* group, and the work of Fouquette (1975) (already discussed) are convincing cases.

Littlejohn, 1965:

The most widely-known case of reproductive character displacement is that of Littlejohn (1965), Loftus-Hills and Littlejohn (1971). The significance and importance of the study is reflected in its discussion in such textbooks as Brown (1975), Wilson (1975), White (1978), Futuyma (1979), Shorrocks (1979). However the same circularity of reasoning applies in this case as in the others previously discussed. Littlejohn (1965) remarks that since sympatric populations exhibit a marked difference in characters such as pulse repetition frequency 'It is suggested that the marked differences between sympatric populations have resulted from the direct action of selection ...' He goes on to suggest '... that pulse repetition frequency, because of its similarity in the allopatric populations, and difference in the sympatric populations ... is the critical information bearing component of the mating call on which efficient and specific discrimination depends'. Hence the same argument appears. Pulse repetition frequency is the discriminator because there is divergence in this character in sympatry, and because there is divergence in sympatry then this is evidence for reinforcement.

In contrast to previously discussed cases however Littlejohn in association with Loftus-Hills went on to test the assertion that pulse repetition frequency is the premating isolating mechanism which keeps species distinct. Loftus-Hills and Littlejohn (1971) conducted two choice discrimination trials using synthesized calls with

different pulse repetition rates. The authors reported that in 28 discrimination trials involving eight responsive *Hyla (Litoria) ewingi* females, and seven responsive *H. verreauxi* females, the females were able to discriminate between the two synthetic signals and were attracted by the signal with the pulse repetition rate corresponding to that of their homospecific mating call. However in the production of the synthetic signals the call parameter of pulses per note also changed. The number of pulses in a note of the synthetic *ewingi* call was 15 with 30 pulses per note in the synthetic *verreauxi* call. Loftus-Hills and Littlejohn reject the proposition that this difference provided the basis for call discrimination. They argue that this call parameter will seem to increase as the subject approaches the sound source, making such criteria unsuitable for 'interspecific discrimination'. However such a call parameter as the *rate* of change of pulses per note as an individual approaches, could be a quite satisfactory mate recognition signal. It is also quite possible that *L. ewingi* uses pulse repetition rate in the SMRS of that species. If this were so then the results obtained by Loftus-Hills and Littlejohn (1971) would also be obtained.

Blair, 1955:

In this classic paper Blair (1955) began an approach which was to be used in a number of later studies including the ones discussed previously. This is, however, probably the weakest case discussed. In his discussion of the calls of the North American frog species *Microhyla olivacea* and *M. carolinensis*, Blair shows no conclusive evidence that call duration and mid-point frequency of the calls of these species show conclusive evidence for divergence in the overlap zone. Blair is, in fact, quite cautious in his comments: he says (p.477) 'The greater difference in mating call of the two kinds of frogs in the overlap zone, where there is some hybridization, than where the two do not occur together is possibly explained as the result of selection against hybridization'. Later he remarks 'The striking divergence in mating call in overlap zone suggests selection against hybridization' (p.478).

Again the same problem arises here as in the previous cases. Divergence automatically means that the call parameters being considered are isolating mechanisms and this is then seen as evidence for reinforcement. The general point needs to be made that, just as ecological character displacement cannot occur if the two populations do not compete for a particular environmental variability the same applies to reproductive character displacement. If two species do not use the same call parameter in mate recognition then there can be no possible reinforcement. Each of the studies discussed assume that a particular call parameter is 'pre-mating isolating mechanism', i.e. both species actively utilize this parameter in order to ensure that they do not interbreed with members of another species. For this reason, amongst others discussed, it seems to us that there is, at present, no compelling evidence for speciation by reinforcement.

The essential point is this: if there is no good evidence that 'post-mating isolating mechanisms' can directly bring about the evolution of 'pre-mating isolating mechanisms' by selecting against individuals which mismatch with members of another group, and consequently have less fit offspring, then, speciation is indeed most appropriately seen as a reorganization of the system of communication between conspecific males and females.

The so-called semispecies of *D. paulistorum* are then not species in '*statu nascendi*' but distinct species. That hybrids between them are fertile to some degree, does not necessarily mean that they are 'capable of exchanging genes', since Dobzhansky himself agrees that there appears to be no exclusive evidence that crossing occurs in the wild (Dobzhansky, 1972). Dobzhansky (1972) was later to remark that 'A cogent argument can be made, that *D. paulistorum* is really a set of five species'. Dobzhansky

(1972) preferred the interpretation that '*Drosophila paulistorum* is a superspecies which still conserves a common, although deeply fissured, gene pool'. This interpretation then allows for the role of natural selection in producing 'complete premating isolating mechanisms'.

PREDICTIONS OF THE RECOGNITION CONCEPT

The conceptual uniqueness of the Recognition Concept of species is reflected in a set of concise predictions. The testing of these predictions, and any contrasting predictions of the Isolating Concept, is of paramount importance in discussions of the relative merits of these two diametrically opposed concepts. Some of the more important predictions of the Recognition Concept are outlined here.

(a) *Signals and receivers will be structured for efficiency of communication.*

To result in fertilization signals and receivers of individuals of the same species, will be co-ordinated that is, receivers will be 'tuned' so as to 'recognize' conspecific signals. Considerable illustration of this phenomenon has been provided. For example, the studies by Carde and Roelofs (e.g. Carde *et al.*, 1977) on the SMRS's of moths provide details of the use of chemical components in the female sex phenomenon. Males are, however, always 'maximally attracted to a species-specific blend' of these different chemical components.

This prediction is not in absolute conflict with the isolation concept, only that according to the latter view, isolation must result and this may be at the expense of efficiency of communication.

(b) *Stabilizing selection acts on both signals and receivers.*

Individuals which are deviant with respect to either their signal or receiver characteristics are less likely to be recognized as conspecifics and hence will suffer a selective disadvantage. There is considerable evidence for this prediction. In *Drosophila melanogaster*, for example, mutants such as 'yellow' and 'white eye' result in males with deviant courtship (Reed and Reed, 1950; Bastock, 1956) and these are rejected by conspecific females. Similarly, many genes are known to affect the SMRS and these are apparently selectively eliminated from natural populations, as they arise.

(c) *At speciation signals must result in fertilization in the habitat to which the individuals are restricted.*

This basic prediction of the Recognition Concept is in contrast to that of the Isolation Concept. The latter predicts that the design features of signal receiver systems will be primarily dependent upon ensuring effective isolation from other species, i.e. it is the presence of other species in the zone of secondary overlap that is the main force moulding the characteristics of the 'Isolating Mechanisms'.

(d) *The SMRS is expected to show little variation geographically.*

Since the SMRS is co-ordinated and under stabilizing selective pressure minimum variation is expected between geographically distinct populations. Good evidence for this prediction exists from studies on populations of *Drosophila melanogaster* (Henderson and Lambert, 1982; Petit *et al.*, 1976). Similarly Anderson and Ehrman (1967) have shown similar geographic stability in the SMRS of populations of *Drosophila pseudoobscura*.

It should be pointed out that any illustration of geographic variation in frog or bird calls, for example, is not evidence for geographic variation in the SMRS. Recognition is mediated by particular characteristics of the call and these may remain stable despite variation in other components. Emlen's (1972) analysis of playback experiments in Indigo Buntings, together with the results from four other major studies of bird species, stimulated him to comment 'In all five species, recognition depends upon song features that are among the most constant and unvarying in the species

repertoire'. Emlen (1972) also concluded that components of calls which appeared to be involved in individual recognition were extremely variable. Hence variability in calls may be due to the fact that a number of functions are involved.

(e) *The SMRS of any species is likely to remain stable through time.*

The basis for this prediction is essentially the same as that for (d). Once a distinct SMRS has evolved and become fixed, such that individuals from the one group do not recognize those from the original group, and the population then increases in size, we can expect it to remain stable.

(f) *The complexity and specificity of the SMRS will not be dependent upon the presence of sympatric closely related species.*

Isolating Mechanisms need to be more efficient in situations where crossmatings with closely related relatives are possible. Hence, where groups of closely related species occur, selection will strengthen these mechanisms. Alternatively where single species are geographically separated from their relatives, selection will be relaxed. Lack (1974) for example, when discussing plumage of ducks on remote islands, remarked 'There is presumably much less need for such recognition marks on remote islands with only one resident duck species than on the mainland where several species usually occur together'. Mayr (1963: 109) and Sibley (1961) also make similar comments.

In contrast, the Recognition Concept predicts that courtship in such species needs to be equally specific for normal conspecific fertilization to result.

A review of the data available on this point reveals little support for the isolationist expectation. The Black Swan (*Cygnus atratus*) indigenous to Australia, and not sympatric with any other swan species, appears, by all obvious criteria, to possess as complex a courtship as other swan species (Johnsgard, 1965). Even better examples perhaps are the Hawaiian Goose or nene (*Branta sandvicensis*), and the Cape Barren Goose (*Cereopsis novae-hollandiae*). Although each of these species has no close relatives, and appears to have long since split from some ancestral stock, they seem not to lack any of the courtship characteristics of other Geese (Johnsgard, 1965). For further discussion see Paterson (1978).

(g) *Species will remain stable without significant gene flow between populations.*

The suggestion that many species appear to have surprisingly small amounts of gene flow between demes, but retain their species specific characteristics, has worried a number of authors (Ehrlich and Raven, 1972; Grant, 1980; Mayr, 1975). The 'orthodox viewpoint' (Grant, 1980) that 'The steady and high genetic input caused by gene flow is the main factor responsible for genetic cohesion among the populations of a species' (Mayr, 1963: 521-522) is argued to be incorrect. Many species characteristics, including the SMRS, are stable because they are composed of two interdependent parts, i.e. because of their structure. Since the co-ordination between signals and receivers is stable this also results in the stability of species. This stability is so obvious that it has been recognized by non-biologists (Macbeth, 1971).

The Recognition Concept has already been misinterpreted by one author. Templeton (1979) has commented 'The *raison d'être* of a mate recognition system is to prevent matings with other sympatric *Drosophila*', to which Paterson has replied (1980), 'The *raison d'être* of an SMRS is to ensure effective syngamy within a population occupying its preferred habitat'. This basic difference carries with it a different view of the nature of species, how species arise and, indeed, the basic nature of biological diversity.

In conclusion, Dobzhansky's Isolation Concept provided the basis for our genetic investigations of species; perhaps, however, it is time for the adoption of a new framework. The Recognition Concept is a scientifically valid alternative, free of many of the difficulties inherent in the isolation concept and thus deserves serious con-

sideration and testing. It is important to consider this viewpoint because 'The expectations of theory colour perception to such a degree that new notions seldom arise from facts collected under the influence of old pictures of the world. New pictures must cast their influence before facts can be seen in different perspective' (Eldredge and Gould, 1972).

ACKNOWLEDGEMENTS

The authors thank the following colleagues for their useful comments on the manuscript: A. A. Harper, M. J. Littlejohn, D. Roberts, H. L. Carson, Sir Charles Fleming, C. White, S. Dawson, E. C. Young, E. Slooten, M. Ford, J. E. Morton, H. Spencer. D. M. L.'s research is funded by the N.Z. University Grants Committee, Grant No. 140Z88.

References

- ARITA, L. H., and KANESHIRO, K. Y., 1979. — Ethological isolation between two stocks of *Drosophila adiastola* Hardy. *Proc. Hawaii Ent. Soc.* 23: 31-34.
- AVISE, J. C., 1974. — Systematic value of electrophoretic data. *Syst. Zool.* 23: 465-481.
- AYALA, F. J., 1975. — Genetic differentiation during the speciation process. *Evol. Biol.* 8: 1-78.
- BASTOCK, M., 1956. — A gene mutation which changes a behaviour pattern. *Evolution* 10: 421-439.
- BLAIR, W. F., 1955. — Mating call and stage of speciation in the *Microhyla olivacea* — *M. cardinensis* complex. *Evolution* 9: 469-480.
- BROWN, J. L., 1975. — *The Evolution of Behaviour*. New York: Norton and Co. Inc.
- BUSH, G. L., 1975. — Modes of animal speciation. *Ann. Rev. Ecol. and Syst.* 6: 339-361.
- , 1978. — Planning a rational quality control program for the screwworm fly. In R. H. RICHARDSON, (ed.), *The Screwworm Problem*: 37-47. Austin: University of Texas Press.
- CARDE, R. T., CARDE, A. M., HILL, A. S., and ROELOFS, W. L., 1977. — Sex pheromone specificity as a reproductive isolating mechanism among the sibling species *Archips argyropilus* and *A. mortuanus* and other sympatric tortricine moths (Lepidoptera: Tortricidae). *J. Chem. Ecol.* 3(a): 71-84.
- CARSON, H. L., 1978. — Speciation and sexual selection in Hawaiian *Drosophila*. In P. F. BRUSSARD, (ed.), *Ecological Genetics: The Interface*: 93-108. New York: Springer-Verlag.
- DARWIN, C., 1859. — *On the Origin of Species by means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. London: John Murray.
- DOBZHANSKY, TH., 1937. — *Genetics and the Origin of Species*. (1st ed.). New York: Columbia University Press.
- , 1951. — *Genetics and the Origin of Species*. (3rd ed.). New York: Columbia University Press.
- , 1960. — Second Sir William Macleay Memorial Lecture. Bridging the gap between race and species. *Proc. Linn. Soc. N.S.W.* 85(3): 322-327.
- , 1970. — *Genetics of the Evolutionary Process*. New York: Columbia University Press.
- , 1972. — Species of *Drosophila*. *Science* 177: 664-669.
- , 1976. — Organismic and molecular aspects of species formation. In F. J. AYALA, (ed.), *Molecular Evolution*: 95-105. Sunderland, Massachusetts: Sinauer Associates, Inc.
- , AYALA, F. J., STEBBINS, G. L., and VALENTINE, J. W., 1979. — *Evolution*. San Francisco: W. H. Freeman and Company.
- , PAVLOVSKY, O., and EHRMAN, L., 1969. — Transitional populations of *Drosophila paulistorum*. *Evolution* 23: 482-492.
- EHRlich, P. R., and RAVEN, P. H., 1969. — Differentiation of populations. *Science* 165: 1228-1232.
- EHRMAN, L., 1960. — The genetics of hybrid sterility in *Drosophila paulistorum*. *Evolution* 14: 212-223.
- , 1965. — Direct observation of sexual isolation between allopatric and between sympatric strains of the different *Drosophila paulistorum* races. *Evolution* 19: 459-464.
- ELDRIDGE, N., and GOULD, S. J., 1972. — Punctuated equilibria: an alternative to phyletic gradualism. In T. J. M. SCHOPF, (ed.), *Models in Palaeobiology*: 82-115. San Francisco: Freeman Cooper and Company.
- EMLEN, S. J., 1972. — An experimental analysis of the parameters of bird song eliciting species recognition. *Behaviour* 41: 130-171.
- FOUQUET, M. J., 1975. — Speciation in chorus frogs. I. Reproductive character displacements in the *Pseudacris nigrita* complex. *Syst. Zool.* 24: 16-22.

- FUTUYMA, D. J., 1979. — *Evolutionary Biology*. Sunderland, Massachusetts: Sinauer Associates, Inc.
- , and MAYER, G. C., 1980. — Non-allopatric speciation in animals. *Syst. Zool.* 29: 254-271.
- GOULD, S. J., and ELDREDGE, N., 1977. — Punctuated equilibria: the tempo and mode of evolution reconsidered. *Palaeobiology* 3: 115-151.
- GRANT, V., 1963. — *The Origin of Adaptations*. New York: Columbia University Press.
- , 1966. — The selective origin of incompatibility barriers in the plant genus *Gilia*. *Am. Nat.* 100: 99-118.
- , 1980. — Gene flow and the homogeneity of species populations. *Biol. Zbl.* 99: 157-169.
- HARPER, A. A., and LAMBERT, D. M., 1983. — The population genetics of reinforcing selection. *Genetica* 62: 15-23.
- HENDERSON, N. R., and LAMBERT, D. M., 1982. — No significant deviation from random matings of worldwide populations of *Drosophila melanogaster*. *Nature* 300: 437-440.
- IMMELMANN, K., 1967. — *Australian Finches*. London: Angus and Robertson.
- JACKSON, J. F., 1973. — The phenetics and ecology of a narrow hybrid zone. *Evolution* 27: 58-68.
- JOHNSGARD, P. A., 1965. — *Handbook of Waterfowl Behaviour*. London: Constable.
- KANESHIRO, K. Y., 1980. — Sexual isolation, speciation and the direction of evolution. *Evolution* 34(3): 437-444.
- LACK, D., 1974. — *Evolution Illustrated by Waterfowl*. Oxford: Blackwell Scientific Publications.
- LAMBERT, D. M., CENTNER, M., and PATERSON, H. E. H., 1984. — A simulation of the conditions necessary for the evolution of species by reinforcement. *S. Afr. J. Sci.* 80: 308-311.
- , KINGETT, P. D., and SLOOTEN, E., 1982. — Intersexual selection: the problem and a discussion of the evidence. *Evolutionary Theory* 6: 67-78.
- , and PATERSON, H. E., 1982. — Morphological resemblance and its relationship to genetic distance measures. *Evolutionary Theory* 5: 291-300.
- LEVIN, D. A., 1979. — The nature of plant species. *Science* 204: 381-384.
- LITTLEJOHN, M. J., 1965. — Premating isolation in the *Hyla ewingi* complex. (Anura: Hylidae). *Evolution* 19: 234-243.
- , 1981. — Reproductive isolation: a critical review. In W. R. ATCHLEY and D. S. WOODRUFF, (eds.), *Essays in Evolution and Speciation in Honour of M. J. D. White*. New York: Cambridge University Press.
- LOFTUS-HILLS, J. J., 1975. — The evidence for reproductive character displacement between the toads *Bufo americanus* and *Bufo woodhousii fowleri*. *Evolution* 22: 368-369.
- , and LITTLEJOHN, M. J., 1971. — Pulse repetition rate as the basis for mating call discrimination by two sympatric species of *Hyla*. *Copeia* 1971: 154-156.
- MACARTHUR, R., and CONNELL, J., 1966. — *The Biology of Populations*. New York: John Wiley and Sons, Inc.
- MACBETH, N., 1971. — *Darwin Retried: An Appeal to Reason*. Boston: Gambit.
- MALOGOLOVKIN, CH., SOLIMA, A. S., and LEVENE, H., 1965. — A study of sexual isolation between certain strains of *Drosophila paulistorum*. *Evolution* 19: 95-103.
- MAYR, E., 1942. — *Systematics and the Origin of Species*. New York: Columbia University Press.
- , 1970. — *Population, species, and Evolution*. Cambridge, Massachusetts: Harvard University Press.
- , 1975. — The Unity of the Genotype. *Bio. Zbl.* 94: 377-388.
- MECHAM, J. S., 1961. — Isolating mechanisms of anuran amphibians. In W. F. BLAIR, (ed.), *Vertebrate Speciation*: 24-61. Austin: University of Texas Press.
- MOORE, J. A., 1957. — An embryologist's view of the species concept. In E. MAYR, (ed.), *The Species Problem*: 325-338. Washington, D.C.: American Association for the Advancement of Science.
- MULLER, H. J., 1942. — Isolating mechanisms, evolution and temperature. *Biological Symposia* 6: 71-125.
- PATERSON, H. E., 1976. — The role of postmating isolation in evolution. Invited lecture XVth International Congress of Entomology, Washington. Symposium on the 'Application of Genetics to the Analysis of Species Differences'.
- , 1978. — More evidence against speciation by reinforcement. *S. Afr. J. Sci.* 74: 369-371.
- , 1980. — A comment on 'Mate Recognition Systems'. *Evolution* 32(2): 330-331.
- , 1981. — The continuing search for the unknown: A critique of contemporary ideas on speciation. *S. Afr. J. Sci.* 77: 113-119.
- , 1982. — Perspective on speciation by reinforcement. *S. Afr. J. Sci.* 78: 53-57.
- , and JAMES, S. H., 1973. — Animal and plant speciation studies in Western Australia. *J. Roy. Soc. W. Aust.* 56: 31-43.
- PETTI, C., KITAGAWA, O., and TAKAMURA, T., 1976. — Mating systems between Japanese and French geographical strains of *Drosophila melanogaster*. *Japan J. Genetics* 51: 100-107.
- POWELL, J. R., 1978. — The Founder-Flush Speciation: An experimental approach. *Evolution* 32: 465-474.
- RALIN, D. B., 1977. — Evolutionary aspects of mating call variation in a diploid-tetraploid species complex of treefrogs (Anura). *Evolution* 31(4): 721-737.

- REED, S. C., and REED, E. W., 1950. — Natural selection in laboratory populations of *Drosophila*. II. Competition between white-eye genes and its wild type allele. *Evolution* 4: 34-42.
- ROBERTS, D., 1976. — Call differentiation in the *Limnodynastes tasmaniensis* complex (Anura: Lepidodactylidae). Nedlands: University of Western Australia, Dept. of Zoology, Ph.D. thesis.
- RUSE, M., 1981. — Origins of the modern synthesis. *Science* 211: 810-811.
- SHORROCKS, B., 1979. — *The Genesis of Diversity*. London: Hodder and Stoughton.
- VRBA, E., 1980. — Evolution, species and fossils: How does life evolve? *S. Afr. J. Sci.* 76: 61-84.
- WALKER, T. J., 1964. — Cryptic species among sound-producing Ensiferan Orthoptera (Cryllidae and Tettigonidae). *Quart. Rev. Biol.* 39(4): 345-355.
- WALLACE, B., 1968. — *Topics in Population Genetics*. New York: Norton.
- WHITE, M. J. D., 1978. — *Modes of Speciation*. San Francisco: W. H. Freeman and Company.
- WILLIAMS, G. C., 1966. — *Adaptation and Natural Selection*. Princeton: Princeton University Press.
- WILSON, E. O., 1975. — *Sociobiology*. Cambridge, Mass., (Harvard Univ.): Belknap Press.